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A water acquisition strategy may regulate the biomass and distribution of winter forage species in cold Asian rangeland

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Abstract. Aboveground biomass is often restricted by water availability; therefore, water acquisition strategies have important roles in determining biomass volume and distribution under arid conditions. In cold Asian rangelands, the large tussock grass *Achnatherum splendens* is the most important forage for maintaining livestock under severe winter conditions. However, *A. splendens* distribution is restricted to the middle of the slopes of ephemeral streams, making it difficult to manage winter foraging. To understand the mechanisms behind the specific distribution and maintenance of a large *A. splendens* biomass under arid conditions, we established four typical vegetative plots along a riverside slope with different *A. splendens* density levels and elevations: river bottom with no *A. splendens*, riverbank with a large *A. splendens* community, upper slope with an isolated *A. splendens* community, and flat plain with no *A. splendens*. We measured the soil pH and electric conductivity (EC) of the plots and investigated the vertical biomass and root distribution of *A. splendens*. We also investigated the water source for the *A. splendens* communities using isotope techniques. The soil pH was not different among plots, while the soil EC was significantly higher in the river bottom because of salt accumulation. However, low soil EC levels were found under the *A. splendens* communities. In the ground below the *A. splendens* communities, plant stems were buried deeply. The belowground biomass and buried stem depths decreased at the sites of the isolated *A. splendens* communities in the upper slope. The aboveground biomass of *A. splendens* increased as the stem burial depths and, therefore, the adventitious roots depths increased. The water source of *A. splendens* was estimated to be at a depth of more than 30 cm. Thus, *A. splendens* prefers a habitat with a low level of soil salinity and a high level of water availability, which may increase with the sand burial depth because of the increasing accessibility of a substantial water source in the

deeper soil layer. Sand burial may affect the water acquisition strategy and maintenance of large biomasses of tussock grass species that act as important winter forage in cold Asian rangelands.

Key words: adventitious root; community development; dryland; key resource; sand burial.

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Introduction

Aboveground biomass is often strongly restricted by water availability in arid environments, which includes precipitation patterns, soil conditions, rooting depths, and accessibility of substantial water sources (Schulze et al. 1996, Fan et al. 2008). Additionally, in these environments, the water availability is often limited by the soil's salt concentration (Pessarakli and Szabolcs 1999). Soil electric conductivity (EC) could replace soil osmotic potential, and if the EC is greater than 4 mS/cm in the soil, then the growth of non-salt-tolerant species declines (Larcher 2003). Although soil salts usually accumulate on the surface layer, 47% of the root biomass is distributed up to 10 cm underground because it is difficult to extend the roots into consolidated soil and the soil moisture is limited (Ma et al. 2008). However, some species form specific roots for water absorption, such as deep roots for groundwater or adventitious roots after a disturbance (Steffens and Rasmussen 2016) to achieve the substantial water source. The ability to form adventitious roots is advantageous for survival in dry areas with a high frequency of sediment-burial disturbance (Dech and Maun 2005) because the amount of soil moisture in the root zone increases after burial (Maun 1998).

On the cold Asian rangelands, *Achnatherum splendens* (Gramineae), a perennial grass forming dense caespitose with 1.5 m high stems, can provide a windbreak and forage source even when other vegetation is covered by deep snow (Huai et al. 2007, Zhang et al. 2011, 2012, Jamsran et al. 2015), which protect mass livestock losses from harsh winter storms, called *dzuds* (Begzsuren et al. 2004, Tachiiri et al. 2008, Rao et al. 2015). This species is the most important forage and refuge during *dzuds* on the cold Asian rangelands (Fernandez-Gimenez and Allen-Diaz 2001, Huai et al. 2007, Zhang et al. 2012). Pastoralists often protect *A. splendens* communities for use in emergencies (Kakinuma et al. 2013); however, it is predicting that grazing pressure against *A. splendens* communities will increase as the frequency of severe climatic conditions increases (Illius and O'Connor 2000, Kakinuma et al. 2014). To sustainably manage *A. splendens* communities, the mechanism necessary for maintaining and increasing their biomasses, which are conspicuously greater than those of other coexisting species in arid environments, needs to be clarified.

Achnatherum splendens is distributed throughout a wide range of climatic conditions in the Asian rangelands (Feng et al. 2004, Huai et al. 2008, Miehe et al. 2008). Typically, large communities of the species are established on the higher banks of streams and terraces in valleys (de Vries et al. 1996, Zhao et al. 2011). The unique distribution of *A. splendens* may be related to its deeper root extension and the greater availability of groundwater (Fernandez-Gimenez and Allen-Diaz 2001, Zhang et al. 2012). However, the communities become less dense and more isolated on the upper slopes, even in the humid grasslands of northern Mongolia (de Vries et al. 1996). Moreover, the groundwater table in the arid rangelands, such as the Gobi, is extremely lower than those of the humid and warm grasslands. Thus, the differences in water acquisition strategies, including the belowground root distribution patterns, among slope positions (middle and upper), which are considered restricting factors for the specific distribution of *A. splendens* communities in the cold Asian rangeland, remain unclear.

The isotope ratios of carbon and water ($\delta^{13}C$, $\delta^{2}H$, and $\delta^{18}O$) in plants provide valuable information on the water use and source (Busch et al. 1992,

Ehleringer et al. 1992). For example, the carbon isotope analysis provides an estimate of water-use efficiency (WUE) integrated over the time during which the carbon in the plant was fixed (Farquhar et al. 1982, 1989, DeLucia and Schlesinger 1991, Flanagan and Ehleringer 1991, Hanba et al. 1997, Michener and Lajtha 2008, Tanaka-Oda et al. 2010), which also reflects the soil–plant water uptake. Comparisons of the δ^2H and $\delta^{18}O$ values of soil water and the water inside plant tissues can be used to determine the plant's water source (Ehleringer and Dawson 1992, Brunel et al. 1995, Schulze et al. 1996, Ohte et al. 2003, Armas et al. 2010). Isotope measurement can be used to examine the type of water source being used in the maintenance of dense communities of important species, including the large grasses of the cold Asian rangelands.

The objectives of this study were as follows: (1) to clarify the differences in soil conditions among the *A. splendens* communities; (2) to compare water consumption among coexisting species in this area; and (3) to understand the roles of the belowground root distribution and water source in maintaining the aboveground biomass in the arid environment of the Mongolian Gobi steppe. We focused on soil-water availability, as well as salinity levels and the water utilization, between coexisting species and *A. splendens* at the different positions in a slope. We compared soil properties, water sources, and above- and belowground biomasses among *A. splendens* communities from four vegetative plots using isotopic techniques.

Methods

Study site and plot setting

Our study was conducted in the Mandal Gobi Region of Dundgovi Province (45°46′ N, 106°16′ E), Mongolia (Fig. 1). Mandal Gobi is located in the desert–steppe ecological zone. The mean annual precipitation from 2001 to 2010 was 170 mm, with a coefficient of variance of 28%, and the average summer and winter temperatures were 19°C and −14°C, respectively (Sasaki et al. 2008).

In this area, undulation centering on ephemeral streamlines (*wadi*: potential river lines) occurs at lower elevations. The vegetation significantly changes with position along the riverside slope. The dominant species change from halophyte species in lower positions to *A. splendens* or annual forbs in higher positions along the slope. The community size of *A. splendens* also changes with elevation. There is no *A. splendens* at the river bottom, but the largest communities suddenly appear in the middle slope at the riverbank. The *A. splendens* communities become isolates in the upper slope areas, and the flat plains have no *A. splendens*. This distribution pattern is typical in Inner Mongolia and the Mongolian rangelands (de Vries et al. 1996, Miehe et al. 2008). Therefore, we selected four river slopes from different streamlines (except Line 1) with representative vegetation (Fig. 1) and set the four typical vegetative plots as follows: Plot A: valley bottom located in the *wadi*. Halophyte species were dominant in this area, and there were no *A. splendens* communities; Plot B: riverbank with a large and highly dense *A. splendens* community; Plot C: upper slope with an isolated *A. splendens* community; and Plot D: a flat plain dominated by annual forbs with no *A. splendens* (Fig. 2). We measured the relative ground height using Plot A as the base point (Table 1, Fig. 2). The locations and positions of each line and plot are indicated in Figs. 1 and 2. The mean areal coverage (%) of each plant species was recorded from five quadrats (2 × 2 m) that were 1 m apart in the plots (Appendix 1).

Measurement of soil characteristics

To determine the soil pH and electrolytic conductivity (EC) of the study plots, we set five quadrats (2 × 2 m) 1 m apart in every plot, and the soil samples were collected from the surface (0–5 cm) of the four corners and the center of the quadrat and mixed (with five replications per plot). The soil pH and EC were measured using electrodes in 1:5 soil:water suspensions. The soil nitrogen content was measured using an NC analyzer (Sumigraph NC-900; Sumika Chemical Analysis Service, Tokyo, Japan) after drying the samples in an 80°C oven for 5 d.

Measurement of the foliage carbon isotope ratio

To determine the foliage carbon isotope ratio of the plants, we chose a species that had over 3% areal coverage and sampled 1–3 individuals from each plot. The total number of sampled individuals is shown in Table 2. Foliage samples were oven dried at 50°C and ground to a fine powder. The carbon isotope compositions of samples were determined using an isotope ratio mass spectrometer (Delta Plus System; ThermoQuest, San Jose,

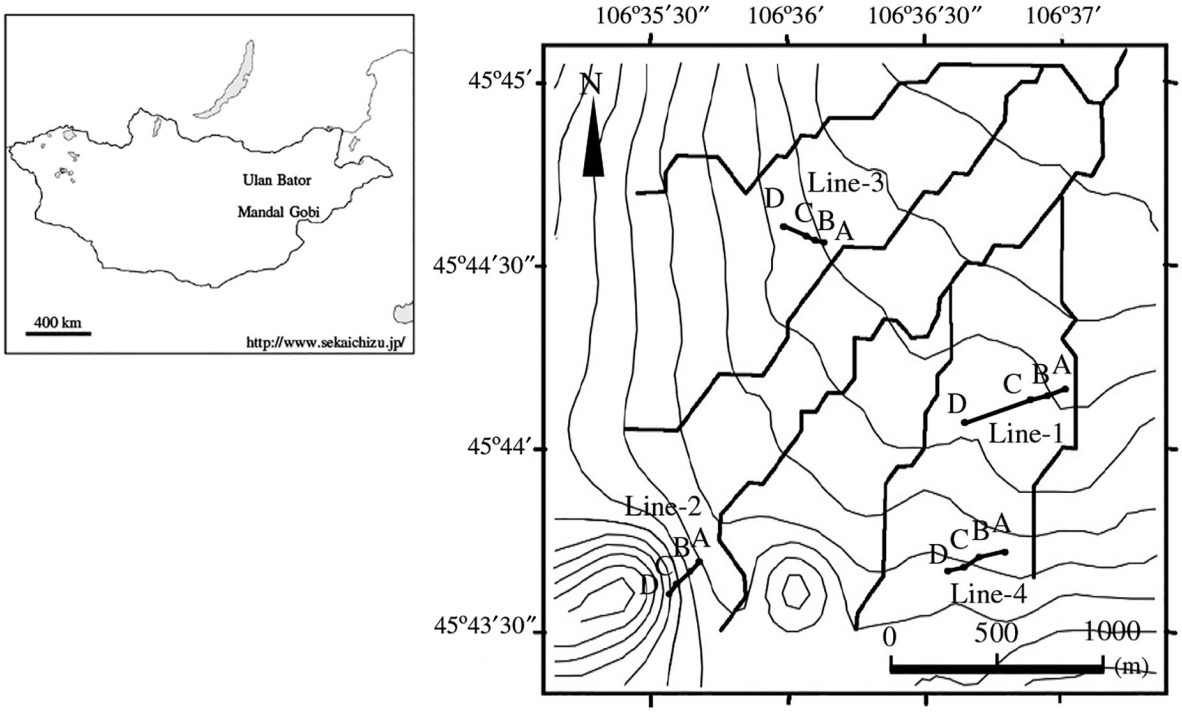

Fig. 1. Locations of the study sites (left) and topographical conditions for the four vegetative plots indicated by A, B, C, and D (right). In the right figure, thick lines indicate potential river lines. Thin lines denote 5-m contour lines. This figure was created by the SRTM 90 m Digital Elevation Database (Jarvis et al. 2008).

California, USA). All carbon isotope ratios were expressed in delta notation relative to a Pee Dee Belemnite standard as follows: $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000$ (‰), where R_{sample} represents the $^{13}C/^{12}C$ ratio of the sample and $R_{standard}$ represents the $^{13}C/^{12}C$ ratio of the standard.

Measurements of A. splendens *biomasses and estimations of stem burial depths*

We set 50 × 50 cm quadrats in *A. splendens* Plots B and C on each of the three transected lines (Lines 2, 3, and 4; with three replications per plot) in August 2013. All of the aboveground leaves and stems of *A. splendens* were harvested. Then, we excavated buried stems and roots. Buried stems were unearthed until the initial point appeared (Fig 3), which was considered to once be the soil surface. We measured the stem burial depth from the soil surface to the initial point in 9–15 individuals per plot. We collected roots and buried stems separately from 20 cm depth intervals. Each part of the plant was dried for more than 48 h in a 60°C oven, and the dry weight was measured.

Estimating water sources of A. splendens

We compared the values of stable isotope ratios of oxygen 18 and 16 of the soil- and plant-extracted water to determine the water source of *A. splendens*. We choose *A. splendens* communities from Plots B and C at Line 1 in 2011 and Line 3 in 2012. We excavated plant stems from the ground to avoid evapotranspiration effects and soil samples from directly below the stems at depths of 5–10, 10–15, 20–25, and 30–40 cm. Groundwater was only sampled in 2012 because we could not reach the groundwater in 2011, because it was deeper than 2 m, even in the valley bottom (Plot A). It rained the day before sampling Line 3 in 2012, and we sampled the rainwater. All soil and plant samples were placed in glass vials immediately after the sampling and sealed with vinyl tape to prevent water evaporation. Water was extracted from soil and plant samples using the cryogenic vacuum distillation method (Ehleringer and Osmond 1989). The stable isotopes of D, ^{18}O, and ^{16}O in the extracted water were measured using a mass spectrometer (L2120-I, Picarro, Santa

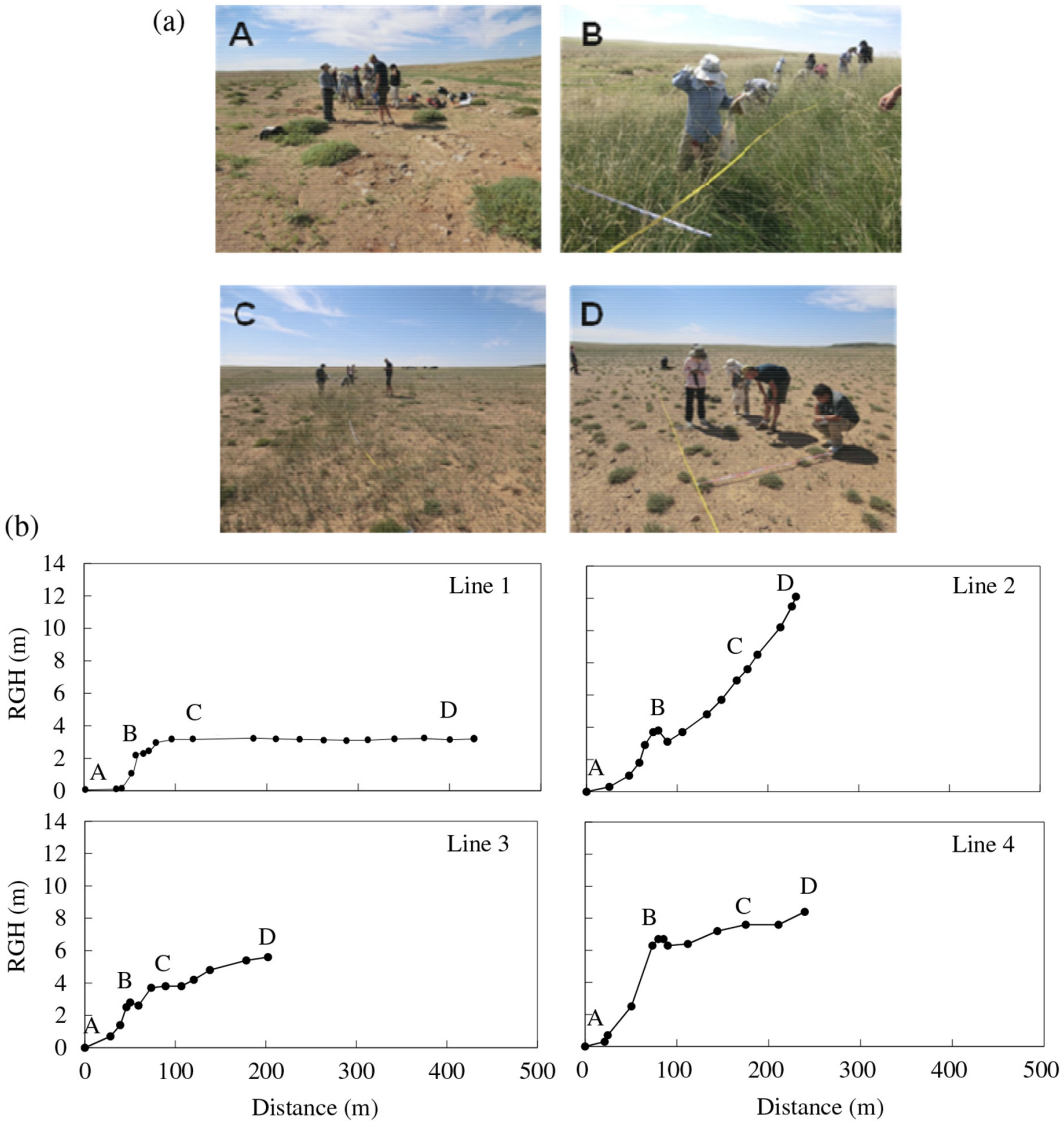

Fig. 2. The appearance of each vegetative plot (a) and relative ground height (RGH, b). Letters in the graphs indicate the positions of each plot; A: valley bottom with no *Achnatherum splendens* communities; B: riverbank with a large *A. splendens* community; C: upper slope with isolated *A. splendens* communities; and D: flat plain with no *A. splendens* communities.

Clara, California, USA). Isotope profiles were expressed in conventional δ units in reference to the international Vienna Standard Mean Ocean Water standard as follows: δ^2H_{SMOW} or $\delta^{18}O_{SMOW} = (R_{sample}/R_{SMOW} - 1) \times 1000$ (‰), where R_{sample} represents the $^2H/^1H$ or $^{18}O/^{18}O$ of the sample, and R_{SMOW} represents the same ratio of the standard. Because the δ^2H signature in plant xylem sap is fractionated by root membranes during water uptake from saline soils (Ellsworth and Williams 2007), we used the $\delta^{18}O$ values to determine the plant's water source.

Statistical analysis

We performed a one-way analysis of variance on soil pH, EC, and nitrogen content among the four plots. The significance of the multiple comparison was determined using Tukey's honest

Table 1. Relative ground heights, topographical conditions, dominant plant species, and soil properties of each vegetative plot (n = 4, means ± SE).

Variable	Plot A	Plot B	Plot C	Plot D
Relative ground height (m)	0	3.9 ± 0.7	5.6 ± 1.0	7.4 ± 1.6
Topographic condition	Valley bottom	Riverbank	Upper slope	Flat plane
Dominant species	*Salicornia* sp.	*Achnatherum splendens*	*Chenopodium acuminatum*	*Chenopodium acuminatum*
Soil characteristics				
Soil texture	Silty	Sandy	Sandy	Silty
pH	9.2 ± 0.5	8.3 ± 0.1	8.3 ± 0.2	8.2 ± 0.2
EC (mS/m)	332.0 ± 67.1[a]	55.7 ± 18.0[b]	42.9 ± 19.3[b]	109.0 ± 74.2[b]
Nitrogen content (%)	0.06 ± 0.00[b]	0.18 ± 0.04[a]	0.09 ± 0.01[b]	0.08 ± 0.01[b]

Note: Different letters indicate a significant difference across the plots according to Tukey's honest significant difference test after the analysis of variance ($P < 0.05$).

Table 2. List of foliage $\delta^{13}C$ values of the plant species that had more than 3% coverage in five experimental quadrats of four vegetation plots.

Plot	Family	Species	n	$\delta^{13}C$ (‰)
A	Amaranthaceae	*Salicornia* sp.	3	−27.8 (0.29)
	Chenopodiaceae	*Kalidium foliatum*	4	−25.3 (0.80)
		Kalidium sp.	3	−27.3 (0.57)
B	Chenopodiaceae	*Bassia dasyphylla*	4	−27.7 (0.49)
		Chenopodium acuminatum	6	−28.8 (0.30)
	Gramineae	*Achnatherum splendens*	10	−26.7 (0.21)
	Polygonaceae	*Polygonum lapathifolium*	1	−27.6
	Zygophyllaceae	*Nitraria sibirica*	1	−27.3
C	Amaranthaceae	*Suaeda sp.*		C4 plant
	Chenopodiaceae	*Bassia dasyphylla*	6	−27.7 (0.48)
		Bassia sp.		No data
		Chenopodium acuminatum	4	−26.7 (0.33)
		Chenopodium album		No data
	Gramineae	*Achnatherum splendens*	10	−25.5 (0.30)
	Liliaceae	*Allium polyrrhizum*	5	−25.1 (0.29)
D	Chenopodiaceae	*Chenopodium acuminatum*		No data
	Compositae	*Artemisia sieversiana*	3	−27.9 (0.27)
	Convolvulaceae	*Convolvulus ammanii*	3	−25.0 (0.10)
	Gramineae	*Stipa krylovii*	5	−26.4 (0.28)
	Leguminosae	*Caragana leucophloea*	3	−24.0 (0.41)
	Liliaceae	*Allium polyrhizum*	4	−25.0 (0.37)
	Tamaricaceae	*Reaumuria songarica*	1	−24.6

Note: Standard errors are in parentheses.

significant difference test ($P < 0.05$). The differences in WUE between Plots B and C were determined using a t-test ($P < 0.05$).

We used a generalized linear mixed model to evaluate the effects of the aboveground biomass (fixed effect) on the root biomass, buried stem biomass and stem burial depth (independent values), and plot replications included as random effects. We used R version 3.5.1 (The R Foundation for Statistical Computing, Vienna, Austria) and the lme4 library (Bates et al. 2011) for the R statistical programming language to conduct all of the statistical analyses.

Results

Differences in soil properties among four vegetative plots

The soil texture differed among the plots. Silty soil accumulated at the valley bottom in Plot A,

Fig. 3. Adventitious roots from buried stems of *Achnatherum splendens* in the soil (left) and after being exhumed (right). White arrows indicate the concentrated occurrence points of adventitious roots. Black arrows indicate the estimated initial stem point. This sample was taken from Line 3 in Plot B.

and the soil was sandy in Plots B and C, which were located in the middle of the slope (Table 1). The soil pH was highest in Plot A, but there were no significant differences among plots (Table 1). While the soil EC was significantly greater in Plot A than in the other plots, it was especially different from the values in Plots B and C, which harbored *A. splendens* communities. The soil nitrogen content was approximately twofold higher in Plot B than in the other plots (Table 1).

Foliage $\delta^{13}C$ values of plant species

The foliage $\delta^{13}C$ value of *A. splendens* was significantly lower in Plot B (–26.7 ± 0.2‰, $n = 10$) than in Plot C (–25.5 ± 0.3‰, $n = 10$; *t*-test, $P < 0.05$, Table 2). In addition, when comparing the species that appeared in multiple plots, the foliage $\delta^{13}C$ value of *Chenopodium acuminatum* was also lower in Plot B (–28.8 ± 0.3‰, $n = 6$) than in Plot C (–26.7 ± 0.3‰, $n = 4$, Appendix 2). However, the values for other species, such as *Bassia dasyphylla*, did not differ among plots (Table 2).

Above- and belowground biomasses of A. splendens communities

The average above- and belowground biomasses were almost fourfold and twofold larger, respectively, in Plot B than in Plot C (Fig. 4). The stem burial depth was deeper in Plot B than in Plot C (32.0 ± 1.3 cm and 9.9 ± 1.2 cm, respectively), and adventitious roots formed from the buried stems at ~5- to 10-cm intervals from the soil surface (Fig. 3). The aboveground biomass of *A. splendens* did not correlate with the root biomass, while the buried stem biomass and stem burial depth were significantly positively correlated with the aboveground biomass (Table 3).

Water isotope ratio of soil- and plant-extracted water

Using the $\delta^{18}O$ values of soil- and plant-extracted water, we identified the soil layers from

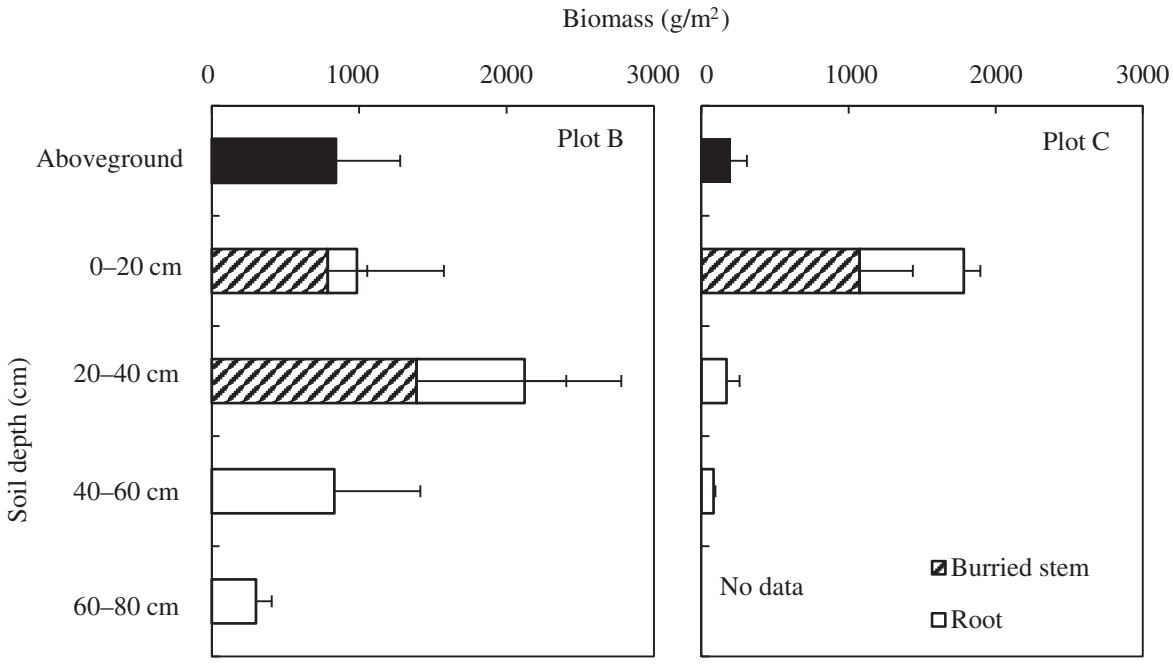

Fig. 4. Above- and belowground biomass amounts of *Achnatherum splendens* in Plots B (left) and C (right). Values are means for Lines 2, 3, and 4 of each plot (n = 3); error bars indicate the standard error.

Table 3. Summary of generalized linear mixed-effects models for *t*-tests using Satterthwaite's method.

	Root biomass			Buried Stem Biomass			Stem burial depth		
Fixed effect	Coeff.	SE	*P*	Coeff.	SE	*P*	Coeff.	SE	*P*
(Intercept)	9.80	5.77	0.27	−4.57	2.37	0.13	−1.26	2.40	0.63
AGB	−0.30	0.19	0.20	0.60	0.14	<0.01*	0.31	0.10	<0.04*

Notes: AGB, aboveground biomass.
* $P < 0.05$.

which the plants obtained their water. The soil water content was slightly higher in Plot B than in Plot C (Fig. 5). The data from Line 3 reflected post-rain conditions. A higher soil water content was found in the surface soil layer compared with in Line 1, and rainwater penetrated and was held at a 15 cm depth only in Plot B (Fig. 5). The $\delta^{18}O$ values of soil water were higher in Line 1 than in Line 3, which reflected ^{18}O enrichment caused by evaporation (Fig. 5; Appendix 2). The $\delta^{18}O$ values of the stems and root-extracted water of *A. splendens* corresponded with the value of soil-extracted water from a 20–30 cm depth in Line 1 of Plot B (Fig. 5). The isotope signatures of plant stem water were significantly lower than any soil water in Line 1 of Plot C. While the $\delta^{18}O$ values of stem water in Line 3 after rain, corresponded to rain and groundwaters in Plots B and C, plant stems showed lower $\delta^{18}O$ values, indicating that they attained soil water from a depth of more than 30–40 cm (Fig. 5).

Discussion

Growing habitats of A. splendens

The growing habitat of the important winter forage *A. splendens* in Mongolian rangelands was significantly correlated with soil condition, which was associated with the level of salt accumulation. In the arid environment, microsite conditions, such as slope position or elevation, affect soil water distributions and especially the soil salinity levels (Zhao et al. 2011). Even when the soil water content is high, lower elevation sites

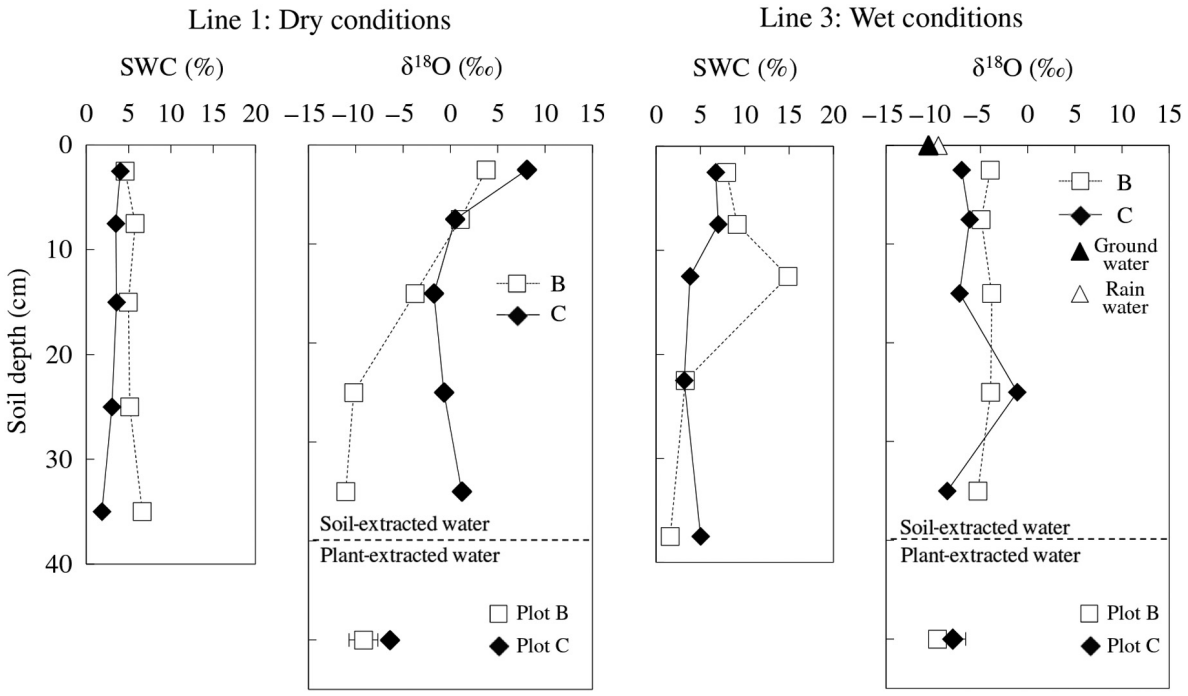

Fig. 5. Soil water content (SWC) and $\delta^{18}O$ values of soil- and stem-extracted water on Lines 1 and 3. Each left figure indicates the SWC (%), and right figure indicates $\delta^{18}O$ values (‰) at different soil depths. The $\delta^{18}O$ values (‰) of stem-extracted water indicate in the lower part of the right figure, and sampling plots are shown in parentheses.

and dent areas with poor drainage accumulate large amounts of salt on the soil surface (Larcher 2003). The existence of halophyte species is a useful indicator of soil salinity (Appendix 1). These species did not exist, or were limited, in the two *A. splendens*-dominated plots, Plots B and C. *A. splendens* is a highly salt-tolerant species in China and Inner Mongolia (Yuan et al. 2011, Zhang et al. 2012), but in fact, the soil EC reported by Zhang et al. (2012) was about one-tenth of the value found at this study site on the soil surface (Table 1). Even if the soil moisture is adequate, the high soil salt concentration, which is too high for *A. splendens* growth, makes its growth difficult in river bottoms and lowlands. Soil texture also correlated to the salt conditions, with fine grain soil promoting salt accumulation. In the middle slope, in which the salinity level was low, sandy soil existed under the *A. splendens* communities (Table 1). This also blocked salt capillary actions and suitable conditions of water penetration at greater soil depths after precipitation (Fig. 5). Barberá et al. (2006) reported the water-holding capacity of the soils was high under the high-dense tussocks because of the slower drying process. The present results of higher soil moisture contents in Plot B rather than in Plot C was also showed higher water availability under the tussock.

The community size of *A. splendens* in the upper river slope may have been restricted by soil moisture availability. The foliage $\delta^{13}C$ values correlate with the WUE (Michener and Lajtha 2007), and the foliage $\delta^{13}C$ values of *A. splendens* communities were higher in Plot C than in Plot B, which indicated stricter water use in the former. The *A. splendens* communities had the greatest unit area biomasses, which must support the high demands of transpiration from leaves. The WUE of *A. splendens* was not significantly different than those of other small-biomass species, and it increased with increasing elevation (Table 2). The soil water content was also low in the upper slope area (Fig. 5). Thus, the requirement of a low soil salinity level because of the high water demand of *A. splendens* might restrict the distribution in the middle slope to avoid the high-salt soil of the river bottom.

The root distributions and water sources of A. splendens *communities*

The development of an *A. splendens* community may be restricted by the ability to absorb water from a substantial water source in the deep soil layers through adventitious roots that are generated from the buried stems. The soil water at greater soil depths is a substantial water source, especially during the dry season in arid regions (Ehleringer et al. 1991, Evans and Ehleringer 1994, Schulze et al. 1996). In the present study, the aboveground biomass of *A. splendens* correlated with the buried stem biomass and stem burial depth (Table 3). The $\delta^{18}O$ values of the *A. splendens* stem- and root-extracted water were similar to values from groundwater at Plot B and from soil water at 30–40 cm below ground at Plot C (Fig. 5). Zhang et al. (2012) reported that *A. splendens* communities occur in areas with groundwater at 1–3 m, with some roots extending to the groundwater. Although our study did not show clearly different isotope signals between rain and groundwater, the groundwater or deeper soil water has a substantial role as a reliable water resource for *A. splendens*.

In this situation, the root penetration capability is a key factor that helps plants to use deep water sources (Li et al. 2013). Sand burial is also a driving force for increasing root depths for some burial-adaptive species (Maun 2004), which increase their aboveground components, such as height or number of leaves (Zhang and Maun 1992, Brown 1997), as well as their dominance (Dech and Maun 2005) and biomass (Martinez and Moreno-Casasolai 1996, Maun 1998). In the present study, the aboveground biomass had no correlation with root biomasses but increased with increasing buried stem depth and, consequently, the depth of the adventitious roots at Plot B (Table 3, Fig. 4). The water source of *A. splendens* was predicted to be deep soil water or groundwater (Fig. 5). Additionally, the concentrations of adventitious roots formed in 5- to 10-cm intervals along buried stems (Fig. 3). While adventitious roots are produced in response to stress conditions (Zhang et al. 2015, Steffens and Rasmussen 2016), this interval may indicate that the root conditions changed discontinuously. From these results, we proposed the mechanisms of community development for *A. splendens* in the Mongolian Gobi steppe. *A. splendens* is mostly distributed along potential river shorelines (Fig. 1; de Vries et al. 1996, Huai et al. 2008) and the lower parts of dunes, where the strong surface runoff or floods water flow brings sand at once every several years by a heavy rainfall (Yatagai and Yasunari 1995). Highly dense and tall tussocks of *A. splendens* are accumulated sand and adventitious roots appear from the stems after sand burial. Finally, sand accumulates under *A. splendens* communities and mounds develop (as seen with Lines 2, 3 and 4 in Plot B; Fig. 2). These are conceivably advantageous for accessing water sources at greater soil depths. Winds also aided in the accumulation of sand in the lower slope area and in higher density tussocks of grass species, such as in Plot B. It is not contradictory to the lack of *A. splendens* in the upper slopes or flat plains, which accumulate less sand, because accessibility to a substantial water source in the deeper soil layer occurs with the increasing buried stem depth.

Conclusion

We examined soil properties and the water source to understand the specific distribution and the mechanisms behind maintaining dense communities of *A. splendens*, which is an important winter forage species of the cold Asian rangelands. The distribution of *A. splendens* in the middle of the valley slope was related to low soil salinity levels and the potential ability to accumulate sand when strong rains occurred. After sand burial, new adventitious roots generate from the stems, and they may be able to access substantial water sources at greater soil depths. The response to sand burial may be a strategy that allows roots to reach deeper depths.

Our results provide an important insight into a key resource species that has the highest biomass among tussock grasses on the cold Asian rangelands. Although some experiments had limited numbers of samples, the results indicated that the specific distribution of large-biomass grass species may be related to securing deep soil water with a low salt level through some climatic or metrological sand-accumulating event. Such a water acquisition strategy may regulate the spatial distribution and biomass of *A. splendens* communities, in a manner similar to sand dune plants (Maun and Susan 1981, Disraeli 1984,

Maun 1998). On the cold Asian rangelands, future climate change is expected to increase the variability in precipitation and the frequency of extreme conditions (Sato et al. 2007, Tachiiri et al. 2008), which will affect the distribution of key resources. Additionally, the grazing impact on key resources increases during meteorological disasters (Huai et al. 2007, Kakinuma et al. 2013, 2014); therefore, climate change and human activity can conceivably accelerate the degradation of *A. splendens* communities.

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